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Growth, Chemistry, and Genetic Profiles of Whitebark Pine Forests Affected by Climate-Driven Mountain Pine Beetle Outbreaks

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Climate change-driven *Dendroctonus ponderosae* outbreaks in semi-naïve *Pinus albicaulis* may result in rapid natural selection for trees with genotypes and phenotypes associated with survival. In this study, we investigated whether survivors were genetically and chemically different from a living cohort of trees that escaped predation due to smaller size and estimated genetic diversity. We also examined how growth rate and climate sensitivity varied between beetle-killed and surviving trees. *Dendroctonus ponderosae* predominantly kills large diameter trees; therefore, we predicted that large surviving trees would have distinctive genetic profiles and, due to bottlenecking and drift, survivors would have lower genetic diversity than the abundant smaller mature trees that escaped predation. We found survivors were indeed genetically divergent from the smaller trees but, contrary to expectations, the smaller trees had lower diversity. This suggests that while beetles may select for trees with particular genotypes, other factors are also driving population genetic sub-structuring. Individual tree terpene profiles were diverse and varied by population but showed no clear relationship to survivorship. Two groups of trees with divergent sensitivities to climate were observed in each population, but neither was a clear indicator of survivorship or susceptibility to beetle attack. Growth rate was the best predictor of survivorship with survivors growing significantly slower than beetle-killed trees over their lifetimes although growth rates converged in years just prior to increased beetle activity. Overall, our results suggest that *P. albicaulis* forests show considerable divergence among populations and within-population genetic sub-structuring, and that they may contain complex mosaics of adaptive potentials to a variety of stressors including *D. ponderosae*. To protect the ability of this tree to adapt to increasing pressure from beetles, blister rust, and climate change, a top priority should be the maintenance of standing genetic diversity and adaptive shifts in allele frequencies.

Keywords: *Dendroctonus ponderosae* (mountain pine beetle), genetic diversity, climate change, adaptation, dendrochronology, *Pinus albicaulis*

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produce different types, amounts, or ratios of secondary chemical compounds that result in the rejection of these trees by beetles but that the chemicals involved are in groups other than the terpenoids we included.

It is not known whether larger resin duct area results in greater constitutive defense. If it does then there should be greater resin flow in slow growing *P. albicaulis*. However, resin flow in *P. albicaulis* is usually very low and sometimes non-existent. During this study, we measured resin flow over a 24-h period in July 2017 for 40 survivors and 40 generals at Vipond Park and only four trees produced measurable, but low, amounts of resin with two falling into each category (data not shown). Additionally, larger resin ducts in other conifers have not been found to result in greater resin flow (Hodges et al., 1981; Hood and Sala, 2015). Slow-growing survivors may invest more in producing greater resin duct area and resin within their xylem, but the effect on beetles may be more qualitative than quantitative, especially if they also invest differently in the secondary chemicals they produce. An investigation into the secondary chemistry of *P. albicaulis* with differing resin duct areas may help identify the means by which beetles can exert 'choice at a distance' given survivors are not attacked and beetles do not encounter resin physically.

Interestingly, climate sensitivity was not predictive of tree survivorship. At Poverty Flat and Vipond Park, beetle-killed trees and survivors both contained large proportions of sensitive and non-sensitive trees (**Supplementary Appendices 2, 3**). Our results agree with those of Cooper et al. (2018) who found no relationship of climate variables to survivorship in *P. contorta* and of Kichas et al. (2020) who found no relationship of these variables to survivorship or resin duct area in *P. albicaulis*.

In correlations comparing BAI/BAs for individual trees and climate variables, again we found no clear difference in climate sensitivity between survivors, beetle-killed trees, and generals (**Table 8**). However, we did find differences between sensitive and non-sensitive trees, particularly a positive correlation to PDSI indicating a negative growth response of sensitive trees to drier conditions (**Supplementary Appendices 2–4**). In contrast, non-sensitive trees did not respond positively to PDSI, but rather, were more likely to positively respond to March temperatures or negatively to December temperatures (CO). Warmer March temperatures may allow for earlier growth in these trees while the negative relationship to December temperature may relate to negative effects of warmer temperatures on snowpack retention. Kichas et al. (2020) observed reduced growth during wetter winters for *P. albicaulis* at a site in northern Montana and Perkins and Swetnam (1996) noted positive responses to winter and spring precipitation on growth of *P. albicaulis* and suggested that feedbacks among climate variables likely produce nonlinear effects influencing snowpack and consequently growth (Perkins and Swetnam, 1996). The sensitive-insensitive dichotomy that we observed in tree responses to climate variables at all three sites further suggests that genetic sub-structuring within *P. albicaulis* populations increases the diversity of tree responses to climatic conditions, potentially increasing resilience of the forest as a whole to fluctuating conditions over time.

There appeared to be a relationship of drought to outbreak development at Poverty Flat and Vipond Park (**Supplementary Figures 2, 3**) but no relationship at Lacy Creek (**Supplementary Figure 3**). In fact, Lacy Creek trees did not reduce growth rates during the most recent drought and actually exhibited dips in growth during wet periods in the 60s and 90s. This highlights the importance of tree responses, and likely genetics, along with climate in outbreak development.

Importance to Conservation

Whitebark pine is in decline across much of its range due to the effects of the non-native disease white pine blister rust, *D. ponderosae* outbreaks, and climate change (Keane et al., 2012). This is a 'wicked problem' in that successful conservation of this tree will require approaches that deal with all three threats. However, as different as these threats are from one another, they share one commonality, and that is that the ability of the species to persist will depend on its potential for adaption to these stressors that, in turn, depends on genetic diversity.

Standing genetic diversity is in large part how long-lived organisms such as trees persist in the face of shifting climatic and other stressors over time (Petit and Hampe, 2006). We found evidence of substantial population sub-structuring in *P. albicaulis* that may indicate a strong adaptive potential. Different cohorts and categories of trees within each population exhibited divergent genetic (**Figure 1**) and phenotypic profiles (**Figures 2, 3**) as well as differential responses to climate (**Table 8**). Older trees possessed greater genetic diversity (**Table 2**) but younger (general) trees grew better under more recent conditions (**Figure 4**) suggesting they may be better adapted to warmer conditions. Although generals had lower genetic diversity, gene flow among other cohorts including large survivors should act to maintain genetic diversity and to produce new genetic combinations on which selection can act. However, the rapid growth rates exhibited by generals may also be a cause for concern given that *D. ponderosae* appears to prefer faster growing trees. This may influence overall stand survival and genetic diversity as these trees reach sizes susceptible to beetle attack. Overall, our results suggest *P. albicaulis* forests contain a complex mosaic of adaptive potentials to a variety of stressors but that the ability of populations to persist will likely vary across the geographic range of the tree depending in the genetic diversity within and among populations (Jorgenson and Hamrick, 1997; Liu et al., 2016).

To protect the ability of this tree to adapt to current and future conditions, the maintenance of genetic diversity should be a top priority, and practices that can reduce diversity or that may introduce maladaptive genes or swamp local adaptation should be avoided. Reliance on natural regeneration is best because it involves locally adapted seed sources drawn from the full array of diversity present in the stand and seedlings that establish will have done so under a local climatic selection filter. Where silvicultural practices are applied, they should be implemented with caution. In cases where planting is required, care should be used in sourcing seed, as even locations close to one another may not be appropriate for collections. For example, trees at Lacy Creek and Vipond Park, located only 27 km apart, showed differences in genetic and terpenoid profiles, growth rates, and sensitivity to

climate. Even when using seed from the site where seedlings will be planted, care must be taken to collect from multiple cohorts, as one cohort may not reflect the full genetic diversity of the site as shown by differences between survivors and generals at our sites. To maximize effectiveness and minimize inadvertent harm, it will be crucial in all conservation efforts to consider the strength of local adaptation and genetic structuring within and among populations as well as the sources and degree of gene flow and the multitude of stressors with which the tree must contend (McKay et al., 2005).

Our results also indicate that thinning prescriptions aimed at increasing tree growth in whitebark pine should be applied with considerable caution. Greater tree ring width/faster growth has been widely used as a proxy for tree vigor and as an indicator of greater resistance to bark beetles (Bhuyan et al., 2017). This view has led to thinning projects in whitebark pine aimed at increasing growth and vigor (Retzlaff et al., 2018) and resistance to *D. ponderosae*. However, while the relationship between growth and resistance to beetles has been shown to be positive in some pines and variable in others (Millar et al., 2012; Knapp et al., 2013; Keen et al., 2020), the opposite appears to be true for some populations of *P. contorta* (Cooper et al., 2018) and for *P. albicaulis*. In our study, as well as in that of Kichas et al. (2020), faster overall growth was the strongest predictor of mortality due to *D. ponderosae* indicating that such treatments will not have their intended effect in *P. albicaulis* and may even be detrimental. Furthermore, naturally low resin production, even by survivor and open-grown *P. albicaulis*, indicates thinning will have little-to-no effect on enhancing constitutive defenses against the insect.

Anthropogenic change is creating or enhancing a number of stressors on forests. To aid forests in adapting to these stressors, we need to move beyond traditional spacing and age-class prescriptions and take into account the genetic variability within and among populations and the impact our actions may have on adaptive potential and forest trajectories. Because so little is known about the genetic diversity in most forest trees, and because it is key to effective conservation, studies of genetic diversity and structuring in forest trees should be a top priority in forest adaptation and conservation efforts.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

DS conceived of the study, participated in all aspects of collections and analysis, and wrote the manuscript. DP did most sample collections in Idaho and participated in project conception and writing. EB did much of the sample processing for genetic and tree ring analysis, and oversaw data management. DS conducted genetic analyses and along with PB conducted the statistical analyses of tree growth and climate with help from JH. GB conducted the chemical analyses while DS, AT, and MH conducted the statistical analysis and interpretations of the data. All the authors contributed to the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.671510/full#supplementary-material

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